

The Reproductive Cycle of the Northern Ravine Salamander, *Plethodon richmondi richmondi*, in the Valley and Ridge Province of Pennsylvania and Maryland

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ABSTRACT

The reproductive cycle, growth rate and age at maturity of *Plethodon richmondi* is here compared with sympatric *P. cinereus* and *P. glutinosus*. Evidence indicates that the cycle differs little from the postulated for *P. cinereus* and northern *P. glutinosus*. All 3 species have biennial cycles, females requiring nearly 2 years to form a new egg complement following egg deposition. All deposit eggs in early summer, probably in late May or early June. As evidenced by spermathecal sperm, mating in *P. cinereus* takes place both in the spring and fall, but courtship in *P. richmondi* may occur primarily in the spring months. In *P. cinereus* and *P. richmondi*, spermatozoa are found only in females having ova of a size capable of being deposited in the spring.

Ovarian follicles in spent female *P. richmondi* may increase in size most rapidly in winter and early spring. Low ovarian egg counts and the presence of resorbing follicles in many females suggest that, as in *P. glutinosus*, population

density may effect reproductive success in some Pennsylvania populations.

Sperm are present in the testes of mature males from September to late April, while the lumen of the vasa remains packed with spermatozoa from late September until late May. Cloacal spermatozoa are found from January to May, and although the vasa are sperm-packed in the fall, cloacal sperm are absent.

Hatching in all 3 species probably takes place in September, although like *P. glutinosus*, the smallest young of *P. richmondi* are not found on the surface until the following spring. Although some juveniles reach maturity at the end of their second summer and males appear to be reproductively active at this time, females most likely do not enter the breeding population until 3 years of age.

The relationship of snout-vent length to weight in *P. richmondi* indicates a change in body form with age.

The ravine salamander, *Plethodon richmondi* Netting and Mittleman, has been recognized as a distinct species since 1938, but its reproductive biology is little known. In southwestern Ohio, Wood (1945) and Duellman (1954) conclude that oviposition in *P. richmondi* occurs between late April and mid-May. Wallace and Barbour (1957) found eggs of *P. r. richmondi* near terminal development in Kentucky and describe the newly hatched

young. Green (1938) and Brooks (1948) report on the eggs and ecology of *P. r. nettingi* in the Cheat Mountains of West Virginia. Short notes on ovarian egg complements have been published by Bishop (1943), Wilson and Friddle (1950), and Seibert and Brandon (1960). No studies on the reproductive cycle in males have been made, and no comparative studies of *P. richmondi* with closely related sympatric species have been published. The pres-

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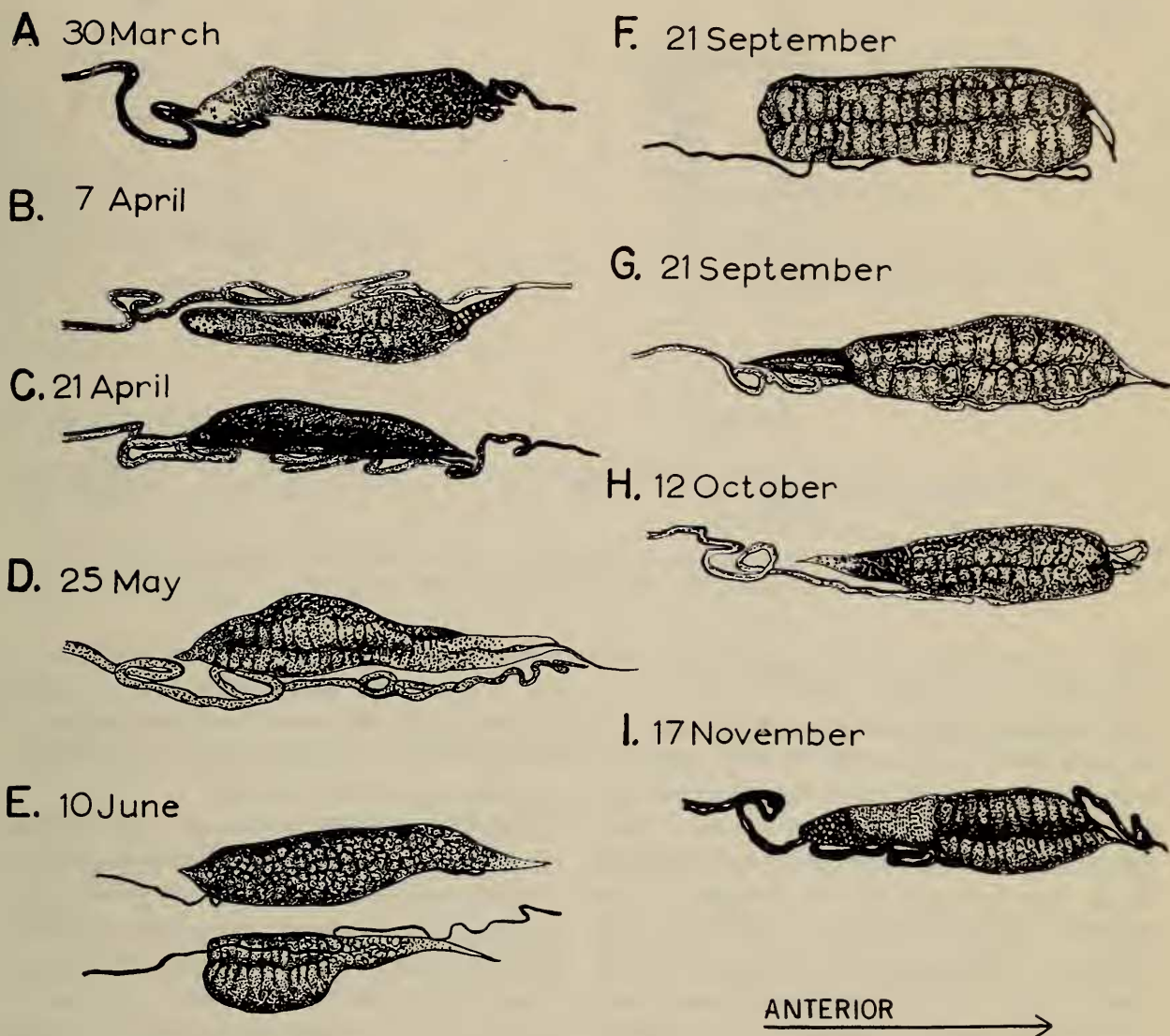


Fig. 1, A-I.—Seasonal changes in the testes and vasa deferentia. Enlarged, lighter areas in the testes are indicative of spermatogenesis or the presence of sperm; darker areas are indicative of evacuation of testicular sperm.

ent investigation was undertaken primarily to compare the reproductive cycle of *P. richmondi* with the studies of sympatric *P. cinereus* and northern *P. glutinosus* as done by Saylor (1966) and Highton (1962), respectively.

This paper is concerned only with *Plethodon r. richmondi* from the Valley and Ridge Physiographic Provinces of Pennsylvania and Maryland. In this area, few *P. richmondi* are active on the surface in late spring and summer and they are usually unavailable from December through late March. For this reason, it

was not possible to observe all stages of the reproductive cycle.

Methods and Materials

Of the 619 *Plethodon richmondi* examined, all but 11 were collected within a 25-mile radius of Hancock, Md. in Bedford and Fulton counties, Pa. and Washington Co., Md. The remaining individuals were taken near Coburn, Centre Co., Pa.

One hundred and eighty-eight salamanders taken during 1963 and 1964 were weighed and measured in the laboratory

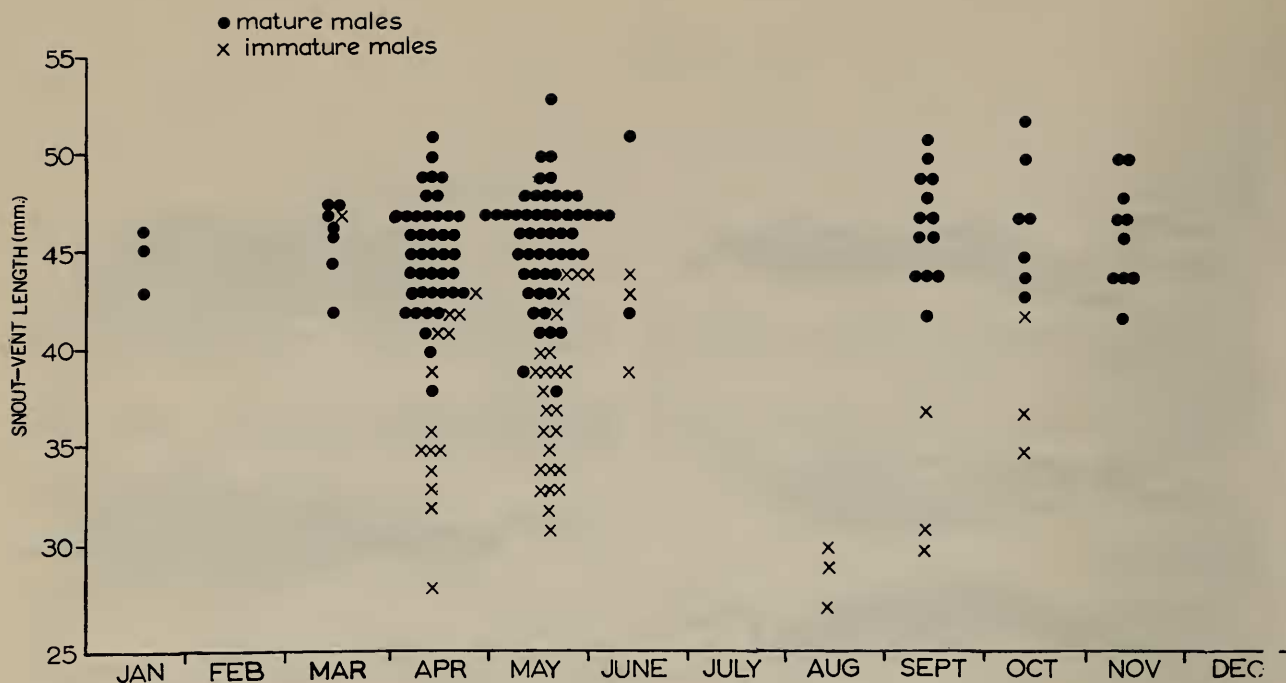


Fig. 2.—Distribution of snout-vent lengths of immature and mature males by month. Circles indicate mature males, crosses indicate immature males.

before preservation. They were kept on wet paper toweling for several hr and were then weighed on a triple-beam balance to the nearest 0.1 g, anesthetized in chlorotone, and measured from the anterior angle to the vent to the tip of the snout (snout-vent length) with a millimeter rule. These data were used to determine the weight-length relationship according to the allometric equation of Simpson et al. (1960: 397). All salamanders were fixed in 10% formalin, transferred to water, and permanently preserved in 65% ethanol.

In *Plethodon*, the testes consist of lobules arranged about a central longitudinal duct. Spermatogenesis, which occurs within the lobules, and transferral of sperm from them to the vasa, proceeds from the posterior to the anterior regions of the testes, producing visible regional changes in size. To determine the progress of this spermatogenetic wave, small pieces of the posterior, mid, and anterior section of a testes and a vas deferens were crushed and examined for spermatozoa. Smears of the cloacal fluid were also examined for spermatozoa.

The number and condition of ovarian follicles were noted and the diameter of

follicles was estimated with a mm rule under a dissecting microscope. The presence of spermathecal sperm was ascertained by examining a crushed portion of the spermatheca with a microscope.

Harding's (1949) method for analysis of polymodal frequency distributions was used to estimate the limits of juvenile age groups. In this method, normally distributed data plotted on probability paper produce a linear distribution of plotted points. A polymodal distribution produces a sigmoidal curve or curves.

Reproductive Cycle in Males

The seasonal changes in the appearance of the testes and vasa deferentia of *Plethodon richmondi* are shown in Fig. 1, A-I. From September to November the testes of mature males are enlarged and have visible sperm-filled testicular lobules. There is a progressive decrease in the diameter of the posterior portions of the testes as spermatozoa are transferred to the vasa deferentia, so that only the anterior portions of the testes remain enlarged by the following January. Complete evacuation of testicular sperm occurs in some males by March and is complete in all males by late April, at

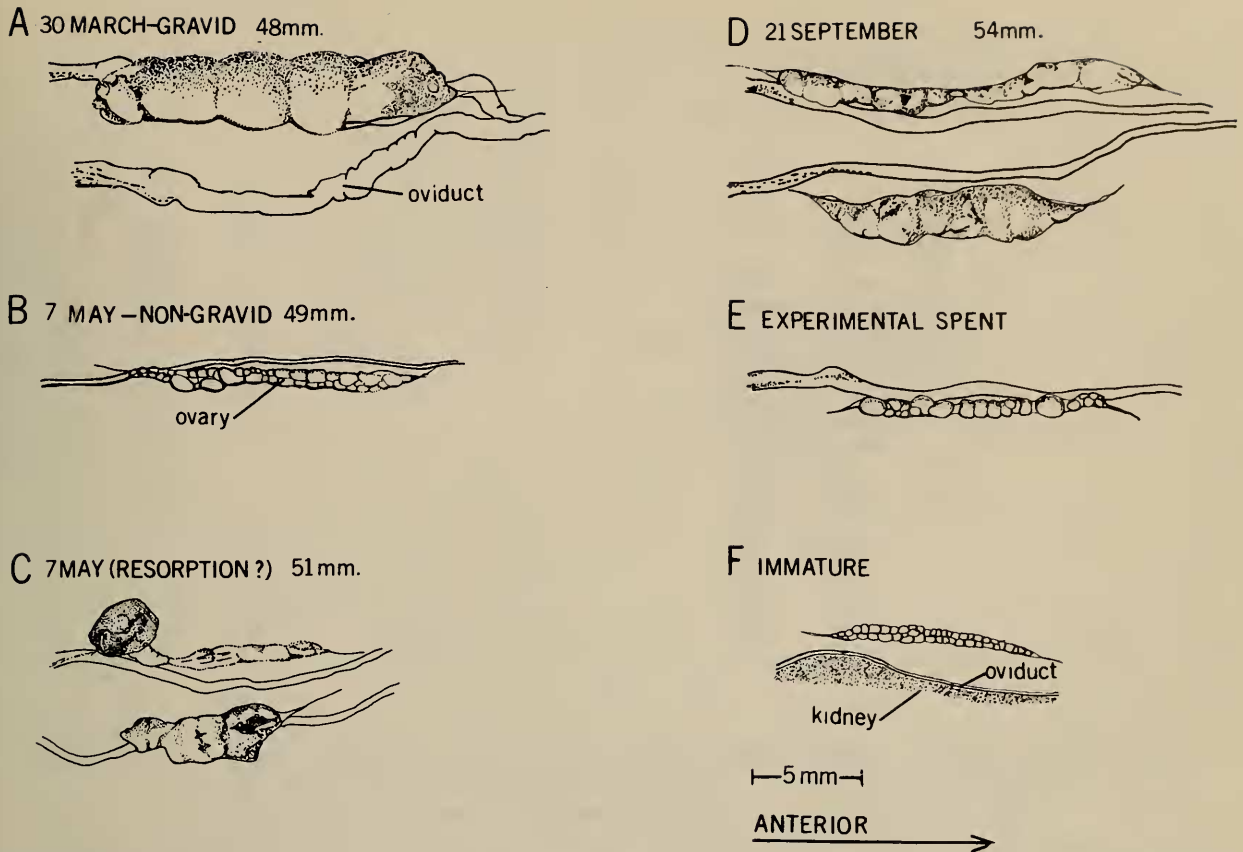


Fig. 3, A-F.—Appearance of the ovary and oviduct of mature, immature, and experimental *P. richmondi*. The date of collection, condition, and snout-vent length are shown where appropriate.

which time the testes appear uniformly small and dark. Regeneration of the posterior lobules, indicated by a slight increase in size, begins in May in some males, although it is probable that maturation of spermatozoa in this region takes place in late July or August.

Spermatozoa are present in the vasa of mature males every month and convoluted sperm-packed vasa are found from late September to May. A decrease in the diameter of the vasa is noted in April and May, as spermatozoa are extruded in the formation of spermatophores. Fifty % of the mature males taken in May have spermatozoa only in the posterior part of the vasa. The vasa deferentia at this time are small in diameter and darkly pigmented.

No intact spermatophores were found in males, but smears of the cloacal fluid frequently contained spermatozoa. Males with cloacal spermatozoa were collected in January (2 of 3) and from March through late May (22 of 74). None of the 28 males examined from September to No-

vember had cloacal spermatozoa, but the enlarged condition of the vasa during this period suggests that spermatophores could be produced in the fall months. Saylor (1966: 191) thought that in *P. cinereus*, spermatophores could be produced from September to May as sperm were abundant in the vasa during that period. Highton (1956: 78), however, implies that in *P. glutinosus* in Florida, sperm-packed vasa were found 6 months before spermatophores were actually produced.

Because sperm were not found in the cloaca of fall-collected males and were found in the spermatheca of only 2 females, mating in *P. richmondi* probably takes place mainly in the spring. Some courtship may also occur in the fall, the extent of which may depend on age of the individual or on such environmental factors as temperature and rainfall. Bishop (1941: 203) suggests that fall rains and warm temperatures may stimulate the production of spermatophores in *cinereus*.

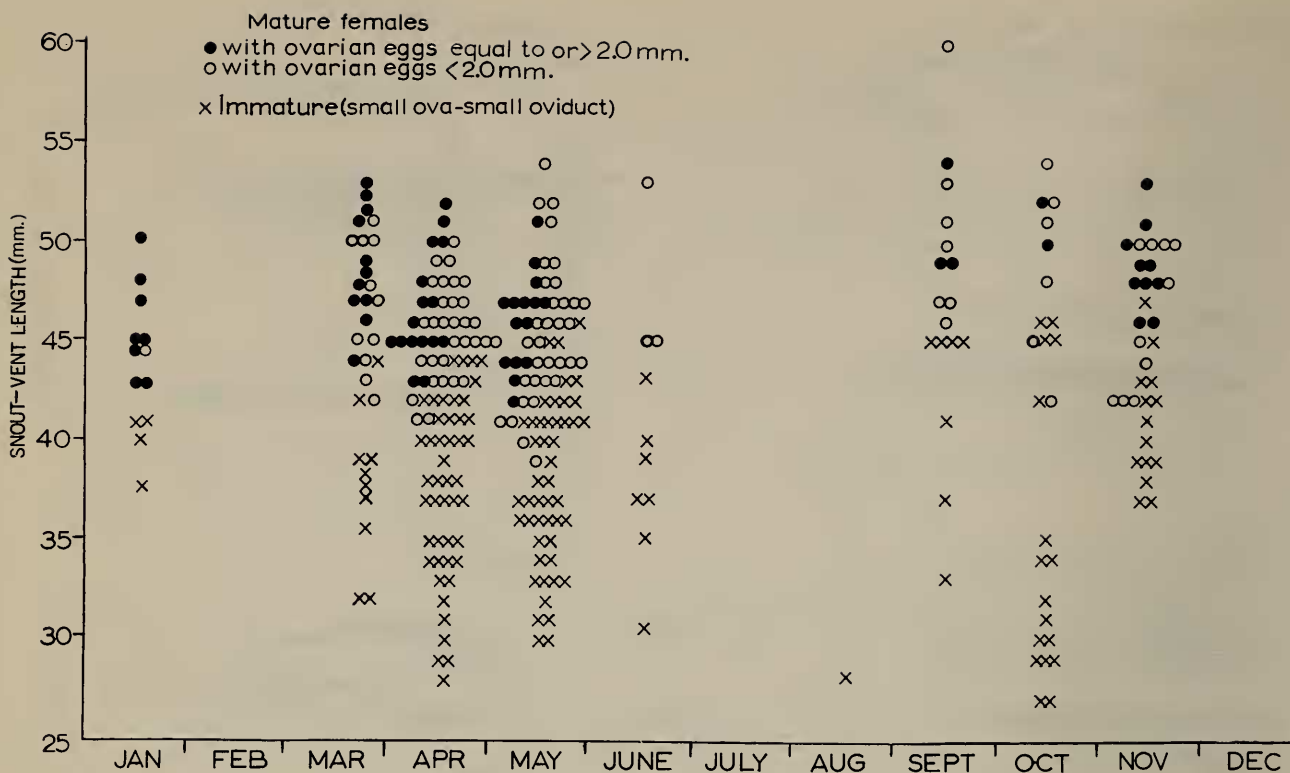


Fig. 4.—Distribution of snout-vent lengths of female *P. richmondi*.

Maturity in males is based on the presence of sperm in the testes or vasa. Pigmentation of the vasa and testes is usually associated with the presence of spermatozoa. However, a male collected in April lacked pigmentation on either testis but had enlarged testicular lobules and sperm in the anterior portion of both. Several males which had only 1 pigmented testis containing sperm had the other testis pigment-free or nearly so, usually lacking sperm.

The distribution of snout-vent lengths of all males collected is shown in Fig. 2. Mature males vary in snout-vent length from 38–53 mm with a mean length of 45.6 mm. Sexable immature males vary from 27–44 mm with a mean of 36.8 mm.

Reproductive Cycle in Females

The overall appearance of the ovary and oviduct of mature and immature females is shown in Fig. 3, A–F. Mature females collected in the spring of the year (January to May) can be placed in 2 classes: 1) those with yellow, yolk-filled ovarian

eggs 2.0–4.0 mm in diameter and large, convoluted oviducts, 2) females of the same size or larger with whitish follicles 1.0–2.0 mm in diameter and smaller, nearly straight oviducts. Mature females usually have the supporting mesotubarium of the oviducts pigmented along the posterior border. Immature females possess clear or whitish follicles 1.0 mm or less in diameter and small oviducts nearly indistinguishable from the kidneys to which they closely adhere. The supporting mesotubarium is unpigmented.

Highton (1962) and Saylor (1966) postulate a biennial cycle in northeastern *P. glutinosus* and *P. cinereus* respectively, basing their conclusions on the presence of mature females without large ovarian eggs in the spring of the year. Both found that post-ovulatory females require over a year to accumulate yolk for a new egg complement, and therefore do not reproduce every year. A similar cycle probably exists in northern *P. richmondi*, where the largest follicles are found in females from January to May, when many mature females (60.4%, $n = 126$) have smaller follicles (Fig. 4).

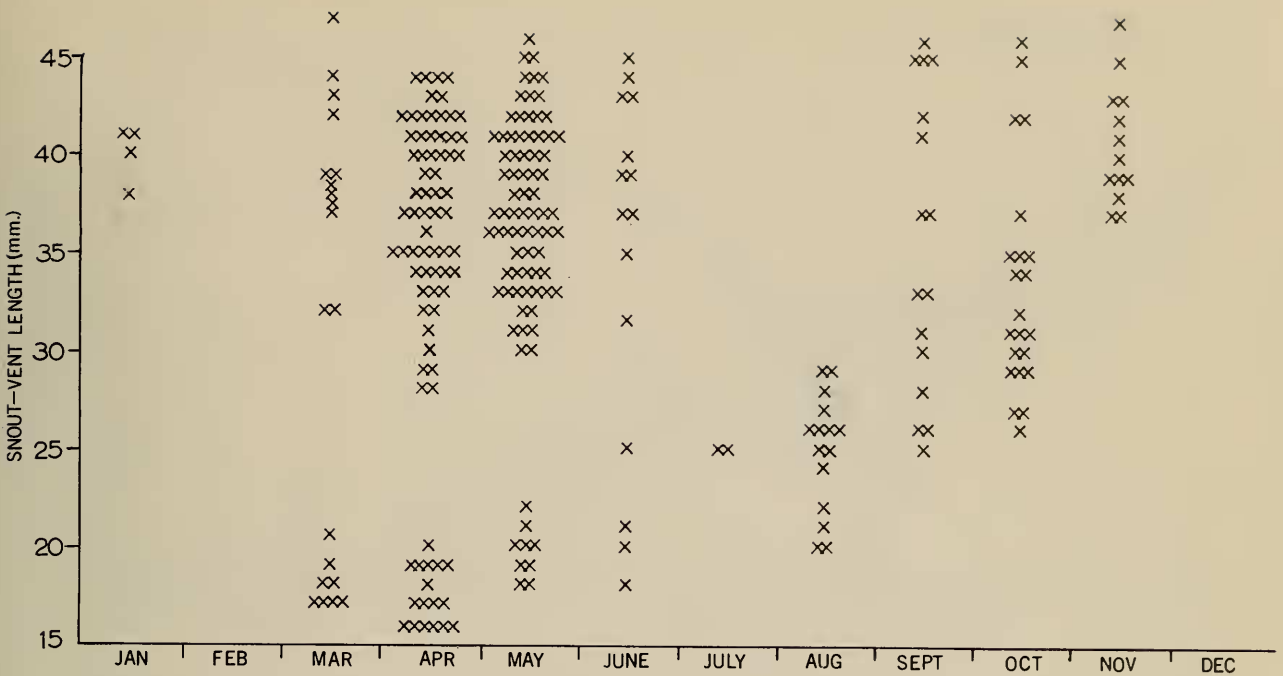


Fig. 5.—Distribution of snout-vent lengths of immature *P. richmondi*.

Sayler followed the growth of ovarian follicles, which range from 0.1–0.7 mm in post-ovulatory *cinereus* collected between August and December. By spring, these follicles are considerably smaller in size than those of gravid females. Following a gradual increase in size throughout the summer and fall, these follicles attain a maximum diameter of about 2.5 mm by October. By their second spring, these ova measured between 2.0 and 3.0 mm, when presumably, they are deposited.

In *P. richmondi*, the separation in the size of ovarian follicles between gravid and nongravid mature females is not as clear as in *P. cinereus*. Follicles range continuously from less than 0.5 mm to 4.0 mm in diameter. Also, there is little indication of growth of follicles less than 2.0 mm in nongravid females during the summer, as follicles found in the fall do not exceed 2.5 mm in diameter. *P. richmondi* may be more efficient in accumulating yolk over the winter than in the summer. Duellman (1954: 43) and Netting (1939: 43) note enlargement of the tails in spring-collected *richmondi*, indicating storage of fat. Since fall-collected specimens had unenlarged tails, Duellman suggests

that in Ohio the salamanders may feed more actively in the winter months.

Although no direct information is available, the following explanation of the ovarian egg cycle in *P. richmondi* is suggested by the monthly condition of preserved females: spent females possess follicles 1.0–1.5 mm in diameter in September when they would be expected to complete brooding. These follicles increase in size during the winter and spring (December to March), accumulating sufficient yolk to measure 2.0 mm in diameter by April and May. At this time, the largest of these follicles overlap in size the smallest follicles of gravid females. Following a period of reduced growth during the summer and early fall, the ovarian eggs measure 2.5 mm by November, and during their second winter, increase to a size capable of being deposited by early summer. Judging from ova in April and May females, the eggs in *P. richmondi* are between 3.0 and 4.0 mm when deposited. These measurements are similar to those given by Bishop (1941: 206) for newly deposited eggs of *P. cinereus*.

Wood (1945: 207) places the time of oviposition for *P. richmondi* in Ohio as

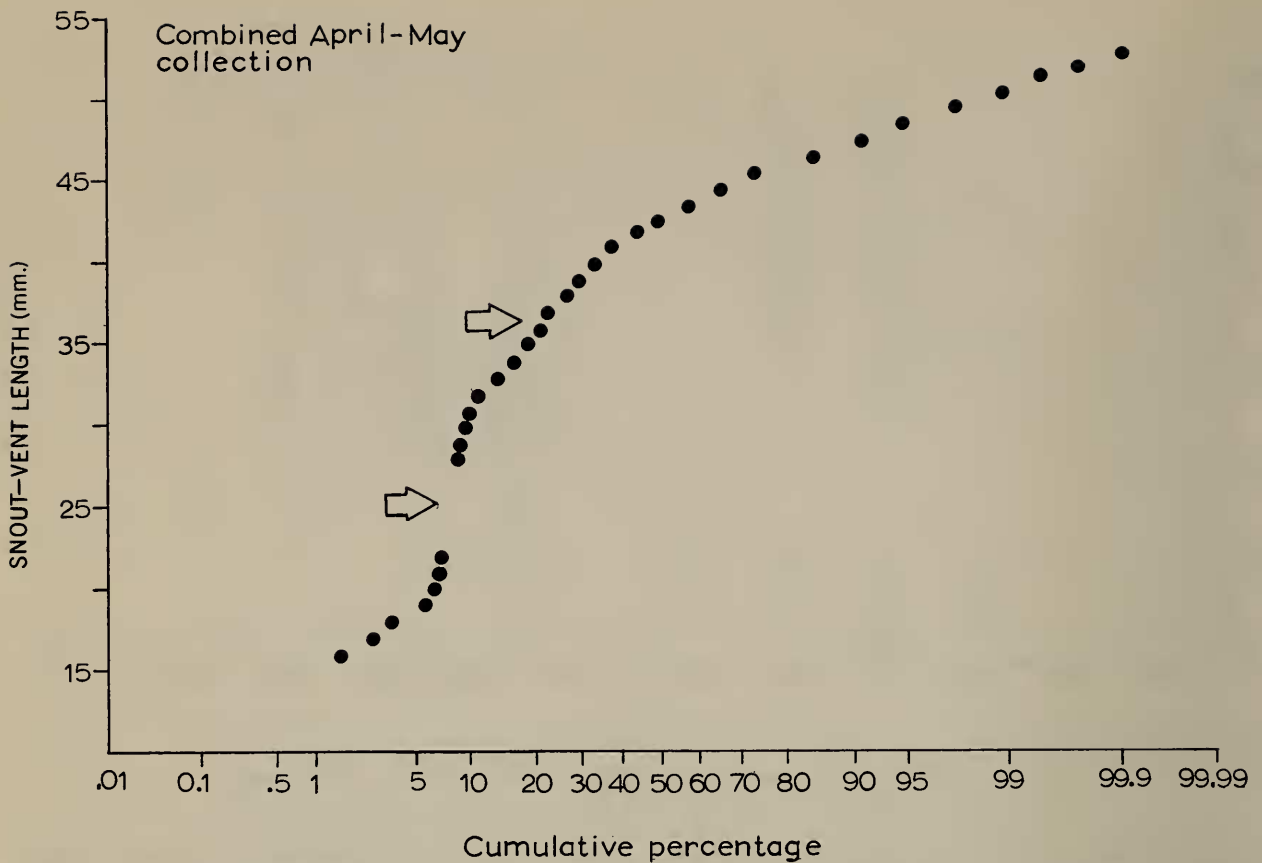


Fig. 6.—Polymodal frequency analysis of snout-vent lengths of the combined April and May collections. Data are plotted on probability graph paper according to the method of Harding (1949). Arrows indicate probable points of inflection.

between 21 April and 14 May. Although the latter date is not unlikely, Wood's interpretation is based on 10 females lacking large ovarian eggs which Wood believes are spent following recent egg laying. Since the total length of these specimens range from 63 to 98 mm, most are probably immature. Of 40 spring-collected females of less than 90 mm in total length which I examined, only 20% are mature. The other females of the group collected by Wood are most likely alternate-year breeders and therefore, would not have enlarged ova. Wood further considers a female collected on 14 May with 5 larger ova (2.5 mm in diameter) to have partially completed oviposition. However, this is well within the normal range of complement size found by Brooks (1948) in *P. r. nettingi*, and may not necessarily represent any reduction due to incompletely laid eggs.

A single *richmondi* egg maintained in the laboratory at approximately 18°C

hatched 61 days after being deposited (Highton, personal communication). Literature records, summarized by Bishop (1941) and Saylor (1966) indicate that the incubation period of northern *P. cinereus* in the field is 6–8 weeks, probably nearer the latter period. Highton's single observation supports the assumption that the incubation period in *P. richmondi* is similar to that of *P. cinereus*. Therefore, the brood of 2 newly hatched young and 2 eggs reported by Wallace and Barbour (1957) in Kentucky on 23 August was probably deposited in June. Duellman (1954: 43) recorded an unattended clutch of embryonated eggs assumed to be those of *richmondi* in Ohio on 14 July. He suggested that these advanced embryos, in some of which the eyes and limbs could be distinguished, were deposited in May, which concurs with the earliest date on which Brooks (1948: 243) found eggs of *P. r. nettingi* in West Virginia (28 May).

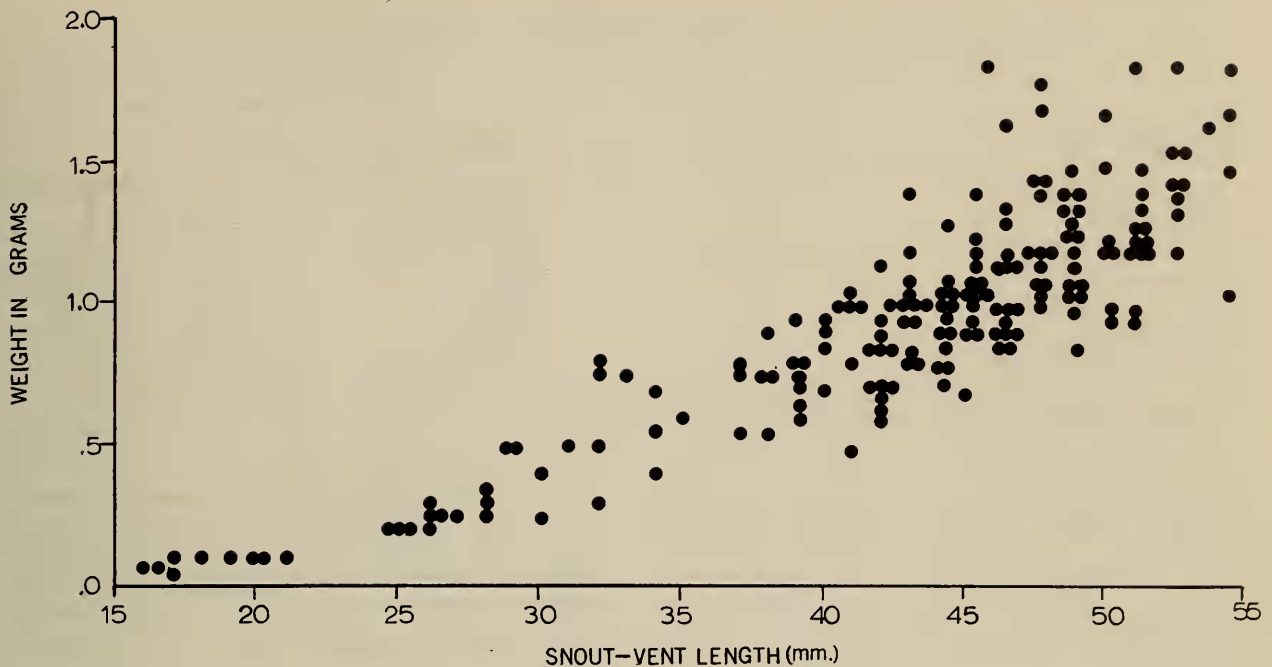


Fig. 7.—Relationship of snout-vent length and weight in 188 specimens, weighed and measured before preservation.

Ovarian egg complements in dissected females and reported clutch sizes vary widely in *richmondi*. In Ohio, Wood found 5–11 ova in spring-collected females; Seibert and Brandon (1960: 299) reported 8 and 9 enlarged ovarian eggs respectively in 2 March-collected specimens. Bishop (1943: 274) examined a female from West Virginia with 7 enlarged ova; Duellman's clutch contained 12 ova. The small number of hatchings reported by Wallace and Barbour may not have represented the original number of the clutch. Brooks (1948: 243), however, found that the number of ova in *P. r. nettingi* ranged from 4–17 in 29 clutches he examined.

Spring-collected females I examined averaged 4.7 (3–8, $n = 39$) enlarging ova per female. This rather small number may be related to population density, as in certain localities in Pennsylvania, *P. richmondi* is abundant and easily obtained during the short period of surface activity in the spring. Anderson (1960: 237) suggests that high density inhibits reproductive activity and lowers brood size in 2 species of plethodontid salamanders in California. Highton (1962a: 601) also suggests that higher population densities may have par-

tially influenced the smaller clutch size in *P. glutinosus* in Pennsylvania females. Anderson found yellow yolk-like deposits in the ovaries and evidence of resorption of follicles. Apparent resorption of ovarian follicles was also noted in *richmondi*. Some females examined had shrunken follicles in which the yolk appeared to have pulled away from the membrane. The membrane could be seen clearly although the follicle had collapsed, and granular orange-yellow or brownish material was frequently present within. Solid, well-filled follicles are sometimes present within such ovaries, as are the usual complement of smaller, white follicles. Females containing ovaries in this condition were collected nearly every month.

Post-ovulatory *P. r. richmondi*, induced to deposit eggs in the laboratory by hormone injection, and recently spent *P. r. nettingi* (collected while brooding in the field) were compared with fall-collected females from Pennsylvania. Spent *P. r. nettingi* females had large oviducts and white ovarian follicles to 1.5 mm in diameter although some induced-spent females retained several large yolk-filled ova. Ten females collected in late September from

Table 1.—Snout-vent length (mm) of juvenile *Plethodon richmondi*

Date collected	Number	Range	Mean \pm standard error
March 30–April 12	9	16–20.5	17.7 \pm 0.45
April 30–May 7	21	16–20	17.9 \pm .32
May 21–June 14	8	18–25	20.5 \pm .82
July 8–July 14	2	25	25
August 2–August 3	9	24–26	24.2 \pm .33
^a August 25–Sept. 1	8	24–30	25.5 \pm .71
^a Sept. 18–Oct. 12	16	25–32	28.5 \pm .60

^a Indicates possible overlap with the previous year age class.

Bedford Co., Pa. had somewhat enlarged oviducts and relatively small (1.5–2.0 mm) follicles but were not clearly post-ovulatory. Highton (1956: 85; cf. Fig. 7) found that in Florida *P. glutinosus*, the enlarged oviducts of post-ovulatory females returned to their original size within 2–3 months following oviposition so that they could no longer be distinguished from unspent females.

Spermatozoa are stored in the spermatheca of female plethodontid salamanders from the time of courtship until at least oviposition (Noble, 1931). Sayler (1966: 192) observed that sperm are not found in female *P. cinereus* with ova less than 1.3 mm in diameter. Sayler also determined by histological examination that sperm are not retained by females which had deposited their full egg complement, although a few sperm are found in females which have deposited only a portion of their complement. In spring-collected *P. richmondi*, sperm are present only in the spermatheca of females containing ovarian eggs at least 2.0 mm in diameter. Fifty-one per cent ($n = 41$) of the gravid females collected during the spring (January to May) possess spermathecal sperm. In the remaining females which have large ovarian eggs (3.0 mm and larger), spermathecal sperm are not found, although the dense pigmentation and fibrous nature of the spermatheca made examination difficult. Only 2 of 12 mature females collected in the fall months possessed spermathecal sperm; both contained follicles not exceeding 1.5 mm in diameter. Whether these fe-

males retained sperm from a previous mating is not known, but since only gravid females contain sperm in the spring and neither female appeared to be partially spent, they probably had only recently mated.

Mature females vary from 39–60 mm with a mean length of 47.1 mm. Immature females large enough to be sexed vary from 27–47 mm with a mean of 37.8 mm.

Growth and Maturation

The distribution of snout-vent lengths of all immature specimens is shown in Fig. 5. Although a late summer hatching is indicated in Pennsylvania and Maryland, the smallest individuals (ranging from 16.0–20.5 mm) are collected in March and April, when they are at least 6 months old. Growth of this group during the spring and summer is indicated by the increasing average size in the monthly samples (Table 1). Because of overlap in size with larger individuals of the previous year's age class, growth of the young after September is not clearly indicated.

The 4 newly hatched young of *P. richmondi* found by Wallace and Barbour (1957) in August measure 14–15 mm in snout-vent length. An October-collected recent hatching described by Netting and Mittleman (1938: 43) is between 15 and 16 mm in snout-vent length (23.0 mm total length). Data obtained by Duellman (1954: 44) in Ohio are similar to measurements of juveniles throughout their first year of growth in Pennsylvania and

Table 2.—Summary of known life history of *P. richmondi*, *P. glutinosus* (from Highton, 1962) and *P. cinereus* (from Saylor, 1966).

	<i>P. glutinosus</i>	<i>P. cinereus</i>	<i>P. richmondi</i>
Mating	Probably spring and fall	October–April	Mainly spring, perhaps less in fall
Females breed	Alternate years	Alternate years	Alternate years
Oviposition	Late spring	Probably June	Probably late May–June
Hatching	Probably late summer	August	Probably late August–September
1st appearance of young	April of year following hatching	September	March of year following hatching
Young mature	Probably fall of 3rd year ?	Fall of 2nd year	Males—fall of 2nd year; females—not until third spring
Spermatogenesis begins	April	March	May
Sperm first transferred to vasa	September	August	September

Maryland. A series of 30 spring-collected juveniles which he examined average 17.8 mm in length (16.5–20.5 mm), and he further records the lengths of juveniles collected in September as between 28.5 and 32.5 mm.

The immatures (excluding the young of the year) in the large April and May samples appear to belong to 2 overlapping age groups with modes at about 35 mm and 41 mm. All individuals collected in these months were plotted on probability paper according to Harding's (1949) method (Fig. 6). A change in the direction of a line fitted to the plotted data (an inflection point) suggests the presence of 2 or more normal distributions, each of which alone would produce a straight line. An inflection point, indicating overlap of the young-of-the-year class with animals at least 1 year older, occurs at about 25 mm. A less well-marked inflection point, indicating the broad overlap of immatures with matures, occurs at about 36 mm. The lack of an inflection point within the group of immatures ranging from 28–46 mm indicates that only 1 age group is present. Separate analysis of immature males and females indicate there is no sexual dimorphism in growth rate of juveniles. Most juveniles therefore, probably mature at the end of their second summer or third fall.

Saylor (1966: 190; cf. Fig. 7A) finds that immature *P. cinereus* reach maturity in the fall of their second year, at which time females apparently are capable of mating. Highton (1962: 604) indicates that *Plethodon glutinosus* from central Pennsylvania does not mature until at least 3 years of age and cannot breed until the fourth or fifth year of age. Thus the age of maturity of *P. richmondi* is similar to its close relative, *P. cinereus*, and both differ from the larger sympatric *P. glutinosus*.

Determination of maturity in females is difficult, as the difference between maturing and small, adult non-breeding females is not always great. In the late fall, the small oviducts and ovarian follicles of post-ovulatory females resembles the enlarging oviducts and ovaries of maturing females. Males enter the breeding population slightly before and at a smaller size than do females. Mature males are found in April at 38 mm in snout-vent length, and all but 1 male was mature at 44 mm. As even the smallest of these males have sperm-packed vasa, it is assumed that they are capable of producing spermatophores. The smallest mature female (39 mm) was found in May, but a majority of females were not mature until they reached a length of 43 mm. Most females of this size probably do not enter the breeding popu-

lation until at least their third spring at over 2 years of age, and some females may not mate until their fourth fall at 3 years of age.

Length and weight data (Fig. 7) obtained from those salamanders weighed and measured before preservation were plotted on double logarithmic paper. These data when plotted produced a straight line, indicating that the relationship of weight and length could be expressed by the allometric formula (Simpson et. al, 1960: 397) $W = aL^n$, where W is the weight in grams, L the snout-vent length in millimeters, and a and n constants. For the 188 specimens weighed, the relationship between weight and length is best expressed by the equation:

$$\text{Weight} = 6.26 \times 10^{-6} (\text{length})^{2.606}$$

The weight during growth should increase directly proportionally to the cube of the length (n should equal 3.0), providing the form and specific gravity remain constant. Duellman (1954: 43) found that in adult *richmondi* in Ohio, the tail makes up slightly over 50% of the total length, while in juveniles it constitutes only about 38% of the total length. He also reported differences in the growth rate of the limbs and head.

Table 2 summarizes the known reproductive and life history data for the 3 species of eastern *Plethodon*. The high degree of uncertainty which exists in many areas emphasizes the difficulty in interpreting data based on gonadal conditions of preserved samples, rather than on direct observation in the field. Egg clutches are practically unknown for all 3 species in the area studied.

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